1. COMPRESSED TRIASSIC FRUCTIFICATIONS FROM INDIA, AND THEIR USEFULNESS IN GONDWANAS

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Abstract

There has been increased emphasis on the study of Triassic fructifications from India during the last two decades. *Dicroidium* bearing Triassic beds of Nidpur have yielded excellently preserved compressions of fertile organs in attached and detached forms; these fertile structures associated with their vegetative remains are represented by micro- and megasporangiate organs and exhibit a variety of morphological forms assignable to different plant groups. Systematic studies of the fructifications suggest recognition of major taxonomic groups: *Phycophyta, Bryophyta, Pteridophyta, Pteridospermophyta, Cycadophyta, Ginkgophyta* and *Coniferophyta;* considering the diversities of reproductive structures, found in various groups, strides have been made to trace the ancestral relationships. The possible affiliations of the various fertile and vegetative organs are discussed, based on their distinctive epidermal features, comparative morphology, patterns of arrangements, in situ spore-pollen morphography, seed characters and the distributions of fossils. Epidermal studies of fertile structures enhanced taxonomic resolution is useful for interpreting the systematics and phylogeny. Some enigmatic fertile forms are interpreted as "morphological intermediates" a potential link to Paleozoic relatives and during the course of evolution may have given rise to Mesozoic forms spread over Gondwanic continents. Consistent association of certain fructifications underlines their usefulness in correlation, interpretation of systematics and the time of origin of major groups. *Pteruchus* – a pollen organ is such an example, always associated with leaf – genus *Dicroidium* which is by far the most common, ubiquitous and diverse fructification throughout the realm of Triassic in Gondwana continents. These taxa co-occur nowhere except in regions that were once parts of ancient Gondwanaland. This kind of consistent association can be used to infer the morphoelement comprising the unattached organs. The seed taxon *Savitrispermum* is quite prolific and plays a significant role in the correlation of the Triassic of Gondwana. Also noteworthy is the seed cone *Nidia,* displaying a line of development in the direction of *Cycadales* and elucidates the origin of *zamoid cycads.* Other significant fructifications like *Nidpuria* and *Lelestrobus* are characterized by having *pteridophytic* structural organization but bear *gymnospermous* pollen grains. Likewise, *Bosea* also appears to be an intermediate form because of the pattern of its microsporophyll bearing pendant sporangia somewhat identical with that of *Crossotheca* but it is radically different in bearing costate pollen.

Key words: Paleobotany, Triassic, India.

Introduction

There has been increased emphasis on the study of Triassic fructifications from India during the last two decades. Of the Triassic outcrops in peninsular India, *Dicroidium* bearing Triassic beds of Nidpur have yielded exquisitely preserved compressions of fertile organs in attached and detached forms; these fertile structures,

associated with their vegetative remains are represented by micro-and megasporangiate organs and exhibit a variety of morphological forms assignable to different plant groups. The possible affiliations of various fertile and vegetative organs have been attempted by SRIVASTAVA (1974, 1975, 1990) based on their distinctive epidermal features, comparative morphology, patterns of arrangements, in situ spore-pollen morphography, seed characters and the distribution of fossils. Epidermal studies of fertile structures enhanced taxonomic resolution, which is useful for interpreting the systematic resolution.

Results

Systematic studies of fructifications suggest recognition of major taxonomic groups: *Phycophyta, Bryophyta, Pteridophyta, Pteridospermophyta, Cycadophyta* and *Coniferophyta. Ginkgophyta* is represented by leaf only, no fertile organs have yet been reported.

The algal remains have shown their representation in the form of carbonized filamentous mat-like structure. In some of the filaments, the rounded swellings appeared to be oogonium containing spores which have been described as *Algacites oogonifera.* The presence of oogonia like bodies may be cited as an evidence of their algal nature. However, the oospore is not that distinct (PANT and BASU 1981).

The other non-vascular *cryptogams* are represented by genera *Hepaticites nidpurensis* which evidently has shown an attached sporogonium whereas the other species *H. riccardioides, H. metzeroides* and *H. foliata* have not shown any evidence of fruiting structure. The sporogonium of *H. nidpurensis* when compared with *Cyathodium tuberosum* have shown a similar position on the thalli and their size and oval form are also identical. Also the apical dehiscense in *H. nidpurensis* is a point of resemblance between the two sporogonia but the absence of an involucre around the sporogonium and the lack of elaters inside the sporogonium of *H. nidpurensis* differentiate the fossil genus *H. nidpurensis* from *Cyathodium tuberosum.* The sculpturing of the spore of *H. nidpurensis* have a smooth exine but of *C. tuberosum* are spinous and therefore it could be considered that *H. nidpurensis* might have evolved from the allied forms of thallose *bryophytes* as *Cyathodium.* The lack of elaters, however, of *H. nidpurensis* brings it nearer to that of *Riccia* but the shape of sporogonium of *Riccia* and its complete embedding in the thallus tissue contrast it from former. With this evidence, it could be safely inferred that *H. nidpurensis* might have been an intermediate form in the progressive evolution of thallose *bryophytes.*

The *pteridophytes* have been represented only in the form of occurrence of megaspores of *lycopsid* alliance. However, the present detached sporangium bearing cingulate spores of *lycopsid* affiliations have refuted the contention of the absence of macrofossils of *lycopsida* in the Triassic of India. The taxon is described here as *Krauselitheca* gen. nov. for sporangia bearing cingulate spores. The presence of cingulum in the spores of *Krauselitheca* gives some insight into the evolution of *pteridophytes* at the onset of Mesozoic i.e. Triassic to a fuller understanding of their phylogeny. It also reflects that the giant *lycopods* of Mid–Paleozoic started disap-

Plate 1.1.

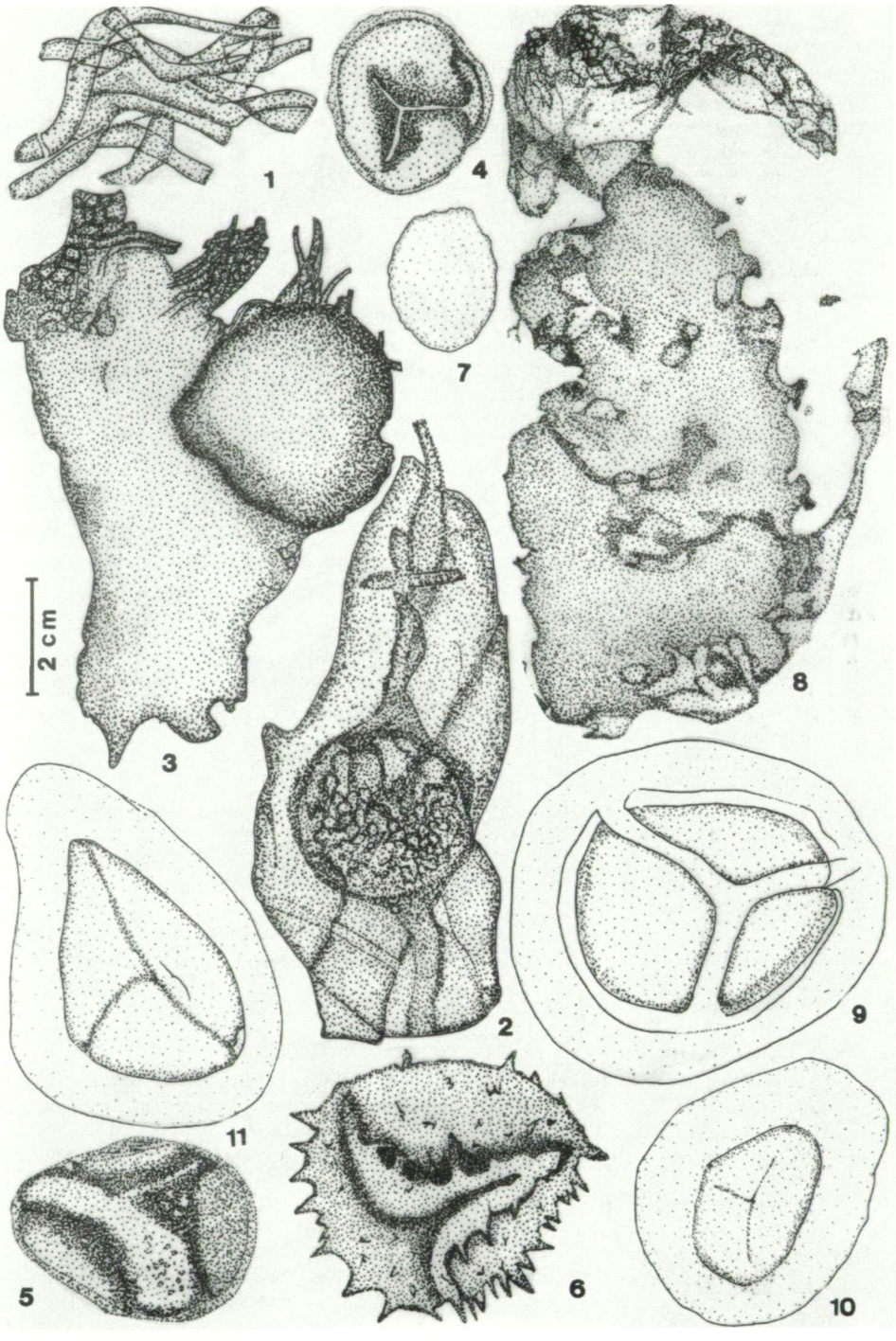
1. *Algacites oogonifera* PANT and BASU 1981. A few filaments of alga showing walls and septa. No: 41305, 2.225x.
2. *Algacites oogonifera* PANT and BASU 1981. Highly magnified view of oogonium-like body showing tuberculate oospore and lateral opening. No: 41306, 990x.
3. *Hepaticites nidpurensis* PANT and BASU 1976. Thallus showing rhizoids and dorsally attached sporogonium. No: 40651, 66x.
4. *Hepaticites nidpurensis* PANT and BASU 1976. Compressed spores obtained after teasing the sporogonium showing a trilete mark. No: 40651, 940x.
5. *Hepaticites nidpurensis* PANT and BASU 1976. Compressed spore, showing a proximal trilete. No: 40651, 940x.
6. *Cyathodium tuberosum.* Proximal view of spore showing spinous exine. 1000x.
7,8. *Krauselitheca* gen. nov. An isolated sporangium in carbonized state immersed in glycerine. No: 10579, 10x, and the macerated sporangium showing sporangial membrane associated with spore mass showing at places liberated spores. Slide No: 10579, 50x.
9–11. Spores retrieved from the sporangium showing cingulum and distinct trilete mark.

Plate 1.2.

1. *Bosea indica* SRIVASTAVA 1975. A branched fructification, showing lateral arrangement of microsporophylls and longitudinally ribbed surface of axis. Holotype No: 85164, 6x.
2. *Bosea indica* SRIVASTAVA 1975. A piece of sporangium wall associated with a few spores. Slide No: 35154–I, 500x.
3. *Rugatheca nidpurensis* PANT and BASU 1977. Compressed sporangia showing striations on the surface. Slide No: 40331. 35x.
4. *Grambastisporites nidpurensis* PANT and BASU 1979. External feature of dry megaspore. Slide No: 41911, 154x.
5. *Srivastavaesporites triassicus* PANT and BASU 1979. Dry megaspore showing sinuous laesurae and well defined arcuate ridges. Slide No: 41021, 84x.
6. *Nidhitriletes spinosa* PANT and BASU 1979. Dry lageniculate megaspores with surface and marginal spines. Distal view. Slide No: 41052, 58x.
7. *Trikonia emerginata* PANT and BASU 1979. A dry trianguloid megaspore showing notches at angles and rounded outline of the inner sac. Slide No: 41040, 100x.

Plate 1.3.

1. *Pteruchus indicus* PANT and BASU 1973. The sporangial head having sporangia. No: 40079, 9x.
2. *Pteruchus gopadensis* PANT and BASU 1979. Central axis showing spirally inserted lateral stalks. No: 40552, 13x.
3. *Bosea indica* SRIVASTAVA 1975. A macerated pendant sporangium with its membranous wall through which spores are visible. Slide No: 35154–8, 100x.
4. *Bosea indica* SRIVASTAVA 1975. A restored branched microsporophyll.
5. *Rugatheca nidpurensis* PANT and BASU 1977. Oval cuticle of an individual sac from a synangium, filled with masses of striate pollen grains of *Rugapites spherica* associated with pieces of outer cuticle. Slide No: 40332, 100x.
6. Pollen grains from inside macerated synangia showing ectexine enclosing endexine. Slide No: 40333, 800x.
7. A pollen grain with an open triradiate slit. Slide No: 40334, 1000x.
8. Endexine of a pollen grain to show triradiate and anastomosing granules giving a reticulate appearance. Slide No: 40334, 1000x.
9. A loose tetrad of pollen grains. Slide No: 40333, 500x.



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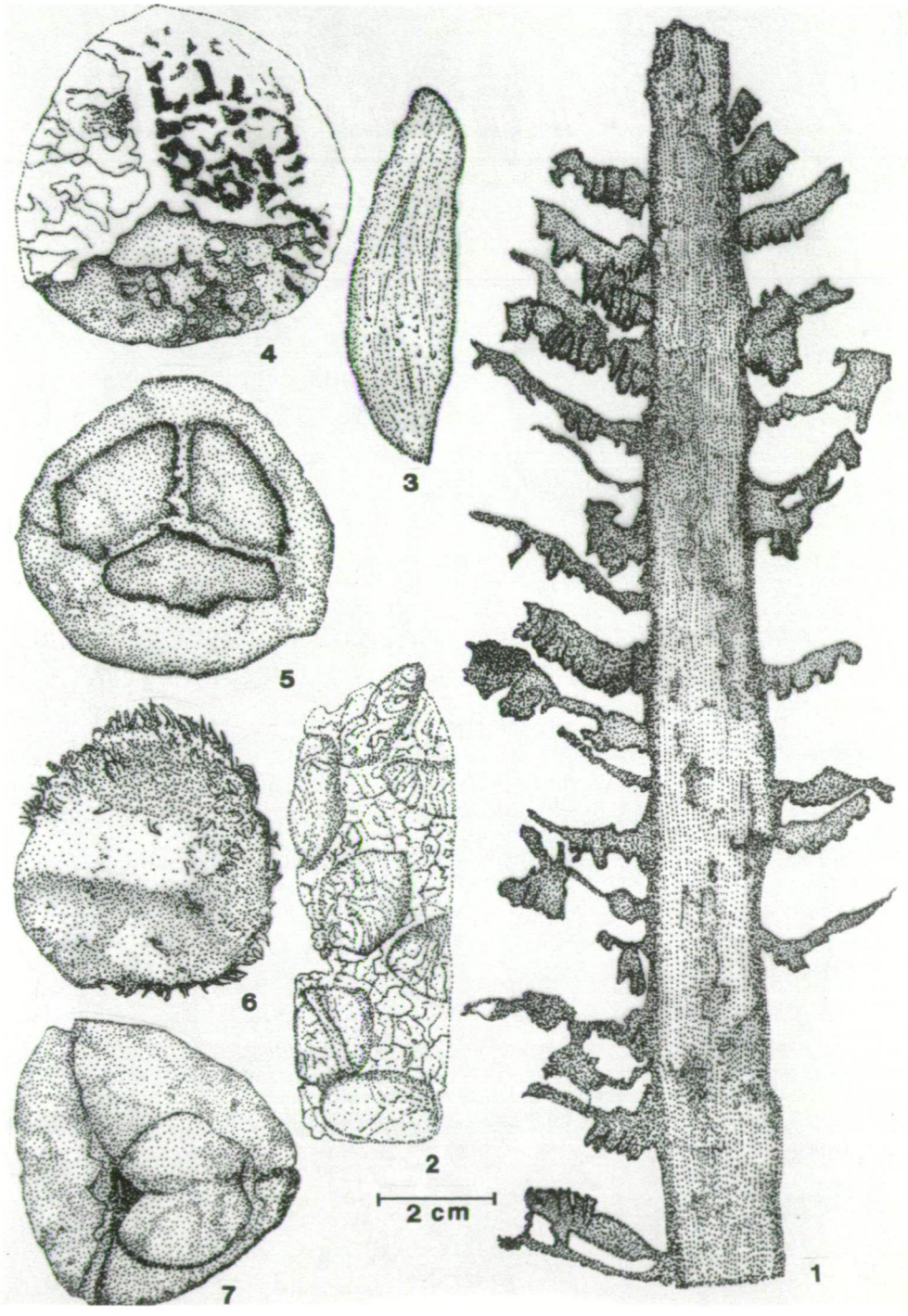

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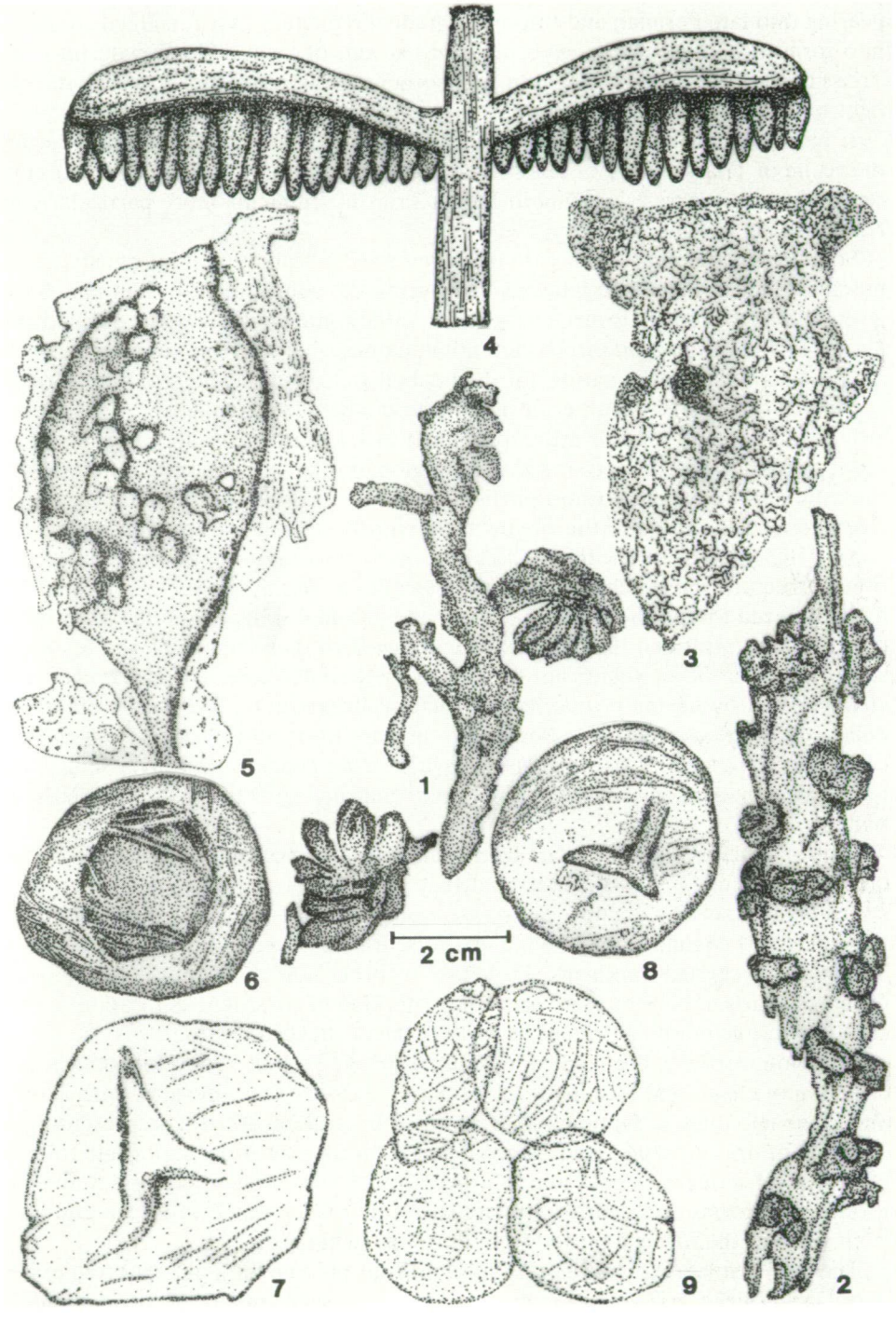


Plate 1.3.

pearing into late Permian and through a gradual reduction they remained confined into form of herbaceous *lycopods* depicting advent of favourable climate into the Triassic. The presence of cingulum is another character of spores which throws light towards the gradual evolution.

It has been obviously observed that throughout Gondwanic continents during the realm of Triassic more or less similar conditions prevailed regarding the occurrence of *pteridophytes* as we find in Indian Triassic sediments more particularly at Nidpur.

Some enigmatic fertile forms are interpreted as "morphological intermediates" a potential link to Paleozoic relatives and during the course of evolution may have given rise to Mesozoic forms spread over Gondwanic continents. Of such forms *Satsangia* and *Birbalsahniostrobus* are notable ones where we find linear microsporangia all synangiate in nature forming a bell or funnel shape structure having sporangial opening on the interior face of the campanulate/stephanate organ. Similarly in the later the entire microsporophyll is arranged in seriate order giving a shape of funnel, bearing sporangial tips conglomerating at the mouth of funnel. All these funnel–shaped microsporophylls are spirally arranged on the cone axis. But characteristically, these fertile organs bear non-striate bisaccate pollen grains depicting their affiliations with the highly evolved forms. However, their organizational structure shows identity with the *medullosan* forms. Therefore, it could be easily inferred that in the evolutionary process residual traits continued from their closely allied forms and thus the newer types evolved thereby making the relationship uncertain. Other significant fructifications like *Nidpuria* and *Lelestrobus* are characterized by having *pteridophytic* structural organization but bear *gymnospermous* pollen grains. Likewise, *Bosea* also appears to be an intermediate form because of the pattern of its microsporophyll bearing pendant sporangia somewhat identical with that of *Crossotheca* but it is radically different in bearing costate pollen.

Consistant association of certain fructifications underlines their usefulness in correlation, interpretation of systematics and time of origin of major groups. *Pteruchus* a pollen organ is such an example, always associated with leaf–genus *Dicroidium* which is by far the most common, ubiquitous and diverse fructification throughout the realm of Triassic in Gondwana continents. These taxa co–occur nowhere except in regions that were once parts of ancient Gondwanaland. This kind of consistent association can be used to infer the morpho-element comprising the unattached organs.

Also noteworthy is the seed cone *Nidia,* displaying a line of development in the direction of *cycads* and elucidates the origin of *zamoid cycads.* Besides, fairly larger and compact cones in Nidpur sediments may be best regarded as representing a complex of ancient cones and some of these forms played an important role in evolution of modern genera and can be interpreted confidently as intermediate forms. Such forms apparently correlate with other Gondwanic countries and also from some of the forms reported from northern hemisphere.

The seed taxon *Savitrispermum* is quite prolific and plays a significant role in the correlation of the Triassic of Gondwana. Its parent seed fructification *Umkomasia* is known from Molteno Formation (Middle-Upper Triassic) of South Africa, a

Plate 1.4.

1. *Pteruchus nidpurensis* SRIVASTAVA 1974. Male fructification, with a group of pollen sacs arranged laterally on a fertile head. No: 35144, 9x.
2–7. Isolated pollen grains from a single sac showing morphological variation. Slide No: 35144, ca 700x.
8. *Pteruchus indicus* PANT and BASU 1973. Specimens showing spirally inserted fertile heads around central axis, some stalks are rendered invisible due to vertically telescoped sporangia. No: 40203, 12x.

Plate 1.5.

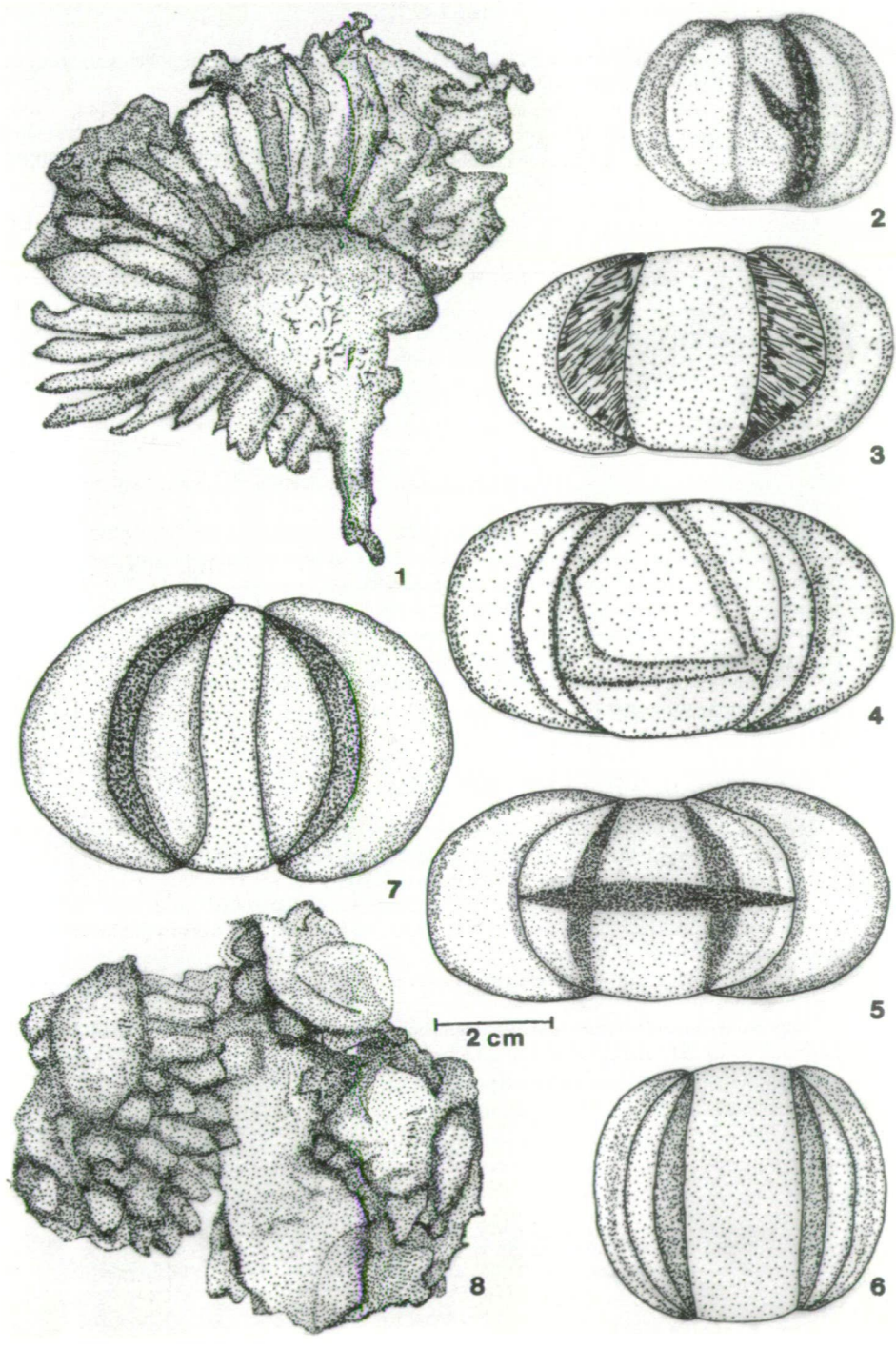
1. *Nidia ovalis* BOSE and SRIVASTAVA 1973. Restortion of megastrobilus of *Nidia ovalis*.
2. Diagrammatic representation of transverse section of megastrobilus *(Nidia ovalis)*.
3. Single megasporophyll with a seed in compressed state.
4. *Urceolaspermum gopadensis* gen. et sp. nov., a compressed seed belonging to *Cycadales*. Slide No: S/1, 10x.

Plate 1.6.

1. *Nidpuria problematica* PANT and BASU 1979. Branched fructification the longitudinal ribs are seen in some portion of axes. No: 40810, 8x.
2. *Nidistrobus harrisianus* BOSE and SRIVASTAVA 1973. A cone bearing microsporophylls, ca 1x.
3. *Nidistrobus harrisianus* BOSE and SRIVASTAVA 1973. A part of microspore bearing cone showing pad shaped sporophylls as seen from the adaxial surface. 1x.
4. *Lelestrobus pennatus* SRIVASTAVA 1984. A microstrobilus showing spirally arranged microsporophylls with its attenuated distal portion. Holotype, No: 35469, 6x.
5. A diagrammatic restoration of a microsporophyll of *Lelestrobus pennatus*.
6. A typical nonstriate, bilateral, disaccate grain showing zone of saccus attachement associated with vertically oblong-ovoid c. b. distally saccus free area recovered from *L. pennatus*. No: 6599/35469, 400x.

Plate 1.7.

1. A reconstruction of *Nidpuria problematica* PANT and BASU 1979.
2. Two winged pollen grains recovered from *N. problematica,* Slide No: 40814, 800x.
3. A large pollen grain with a striated body. Slide No: 40814, 800x.
4–5. Variously compressed four winged pollen grains. Slide No: 40814, 800x.
6. *Rugaspermum insigne* PANT and BASU 1977, a compressed seed with transverse wrinkles on surface and longitudinal ridges. Slide No: 40300, 50x.
7. *Rugaspermum insigne* PANT and BASU 1977, macerated seed showing micropylar canal and pollen chamber. Slide No: 40305, 50x.
8. A compressed seed of *Rugaspermum media* held between the folds of a scale *Equitatilepis elongatus* PANT and BASU 1977, the chalazal hole is facing the apex of the scale. Slide No: 40322, 46x.



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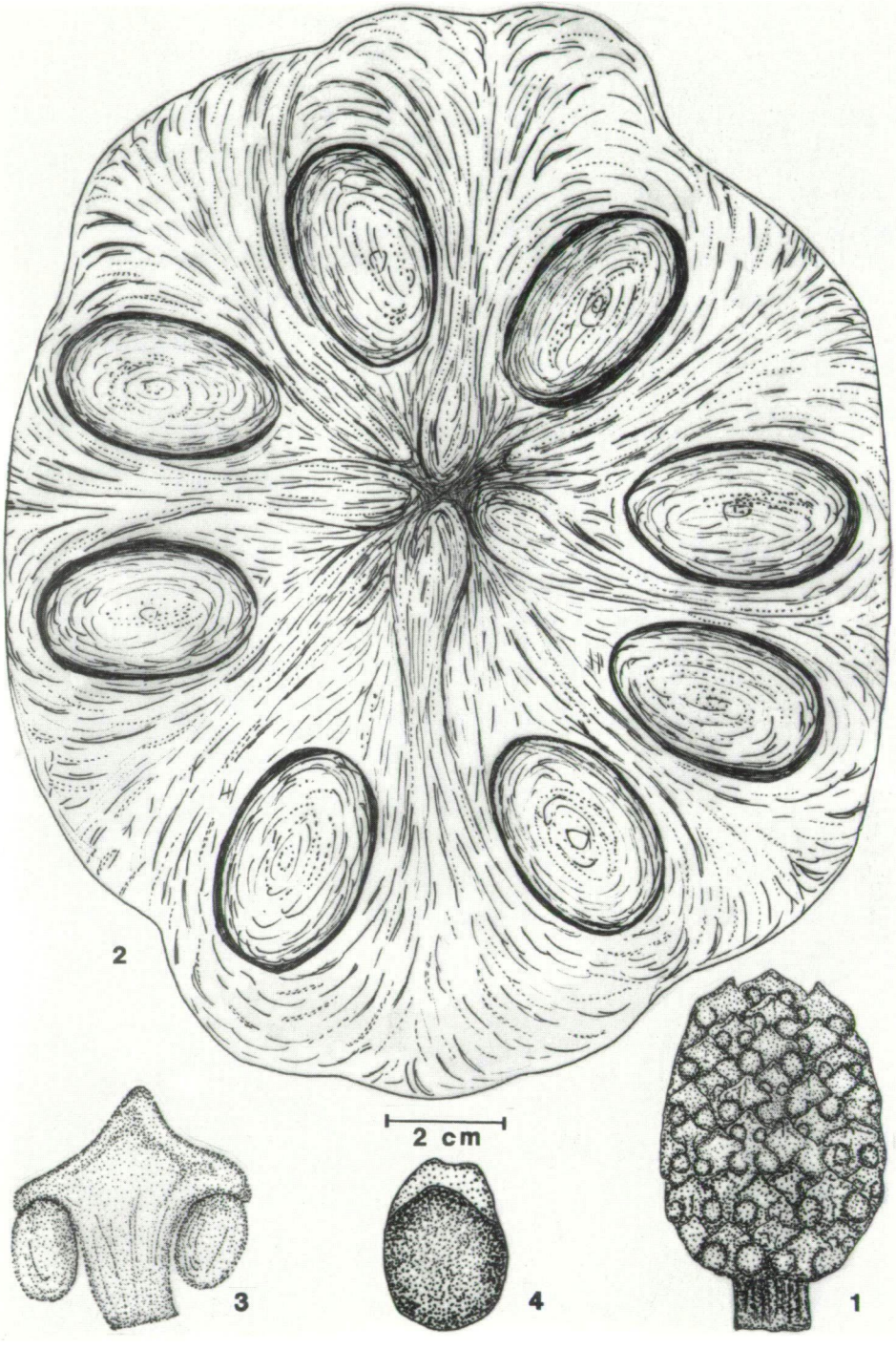

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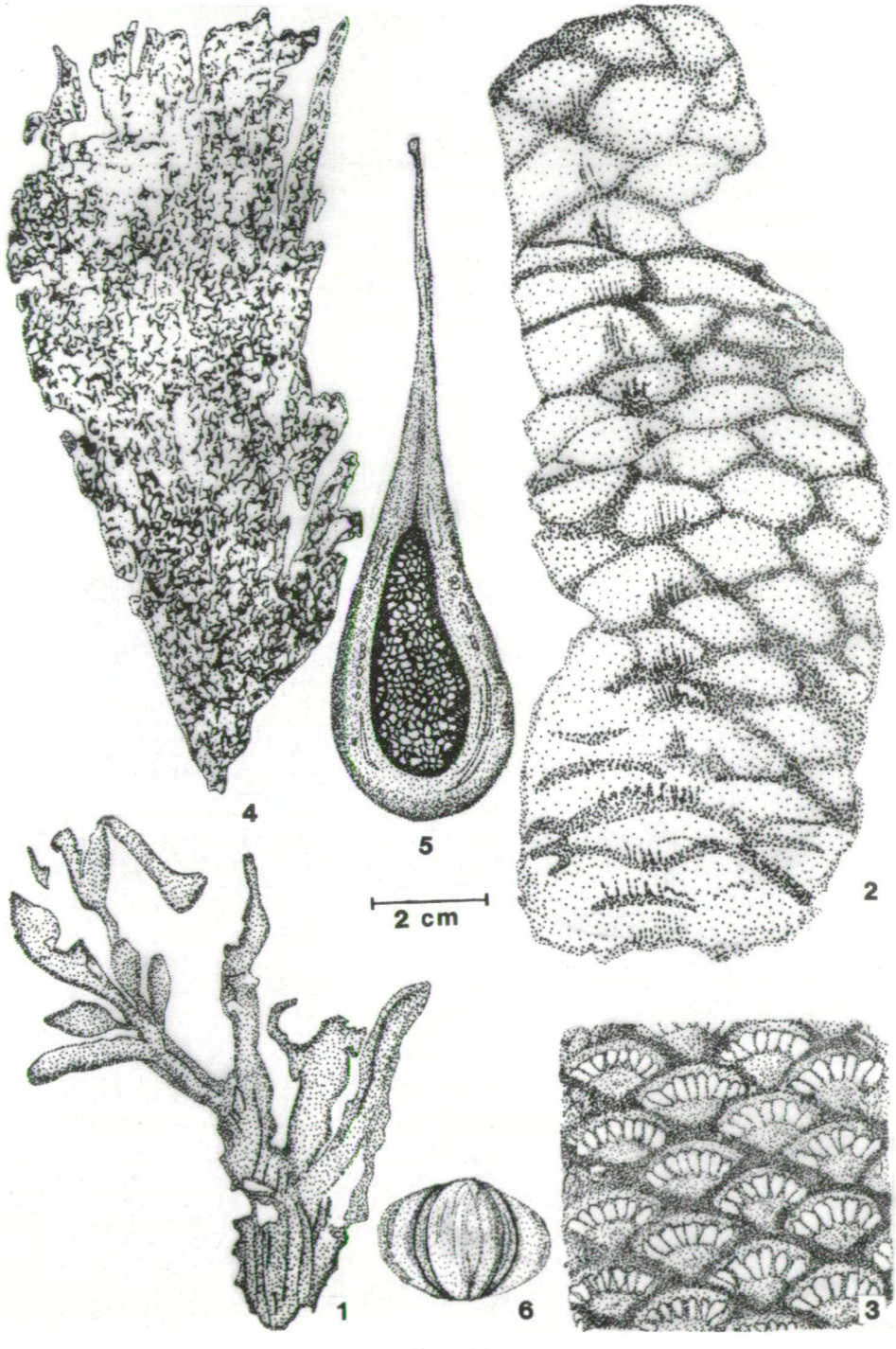

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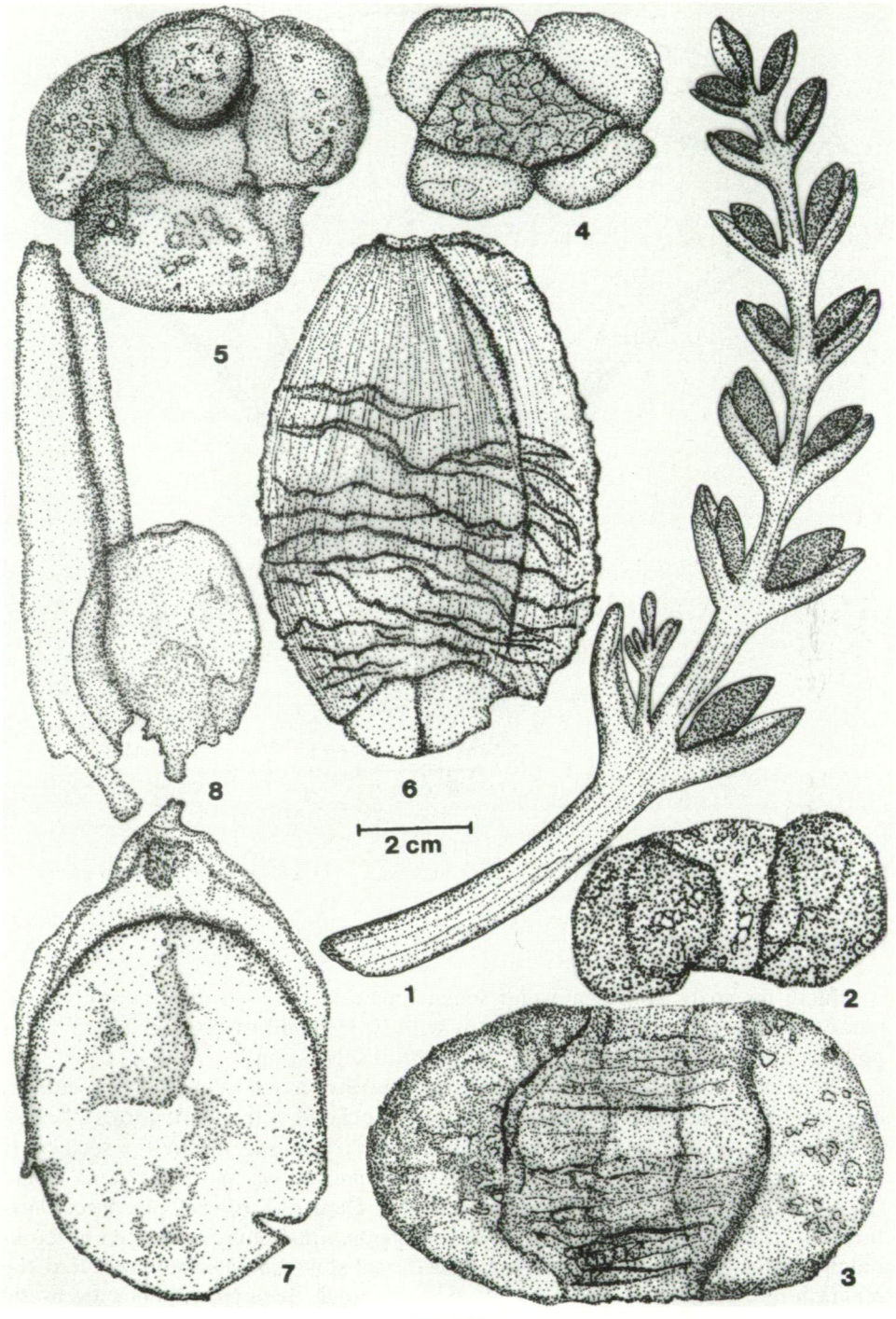

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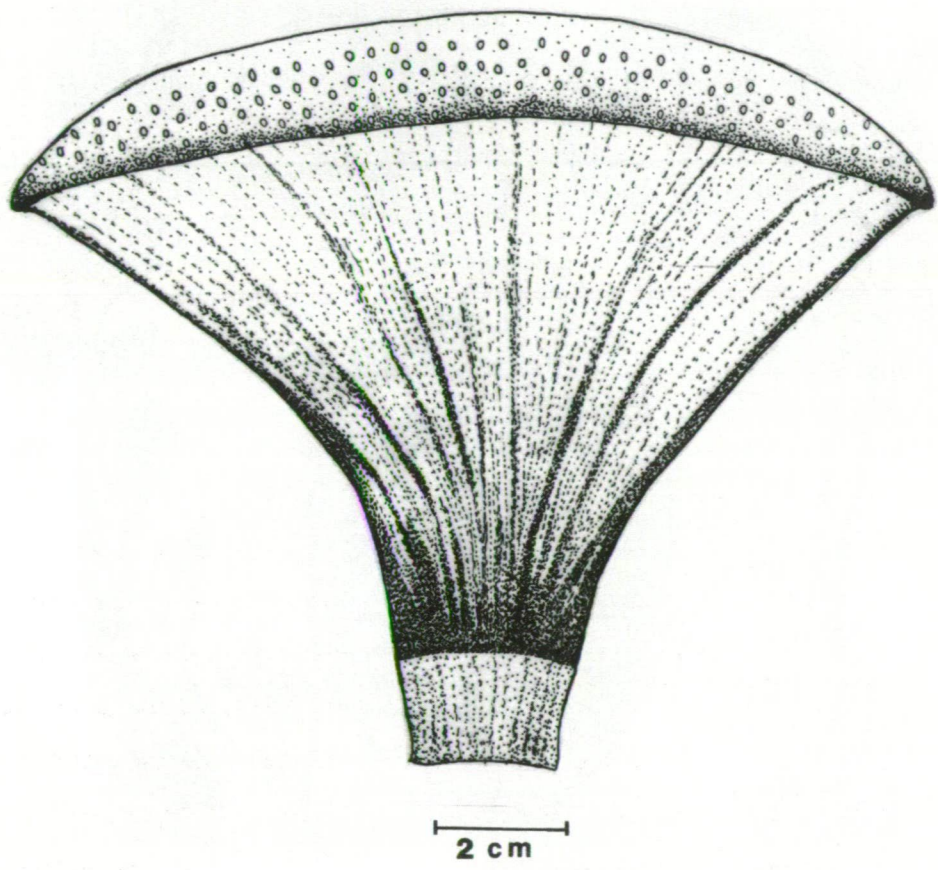

Plate 1.8.
Satsangia campanulata SRIVASTAVA and MAHESHWARI 1973, a diagrammatic reconstruction.

continent far apart from peninsular India. This clearly shows that there occurred parallel formation of similar plants but with little modifications, which could be possible due to geographical and stratigraphical separation.

The evolutionary pattern within the *pteridosperms* has led to most of the features of reproductive biology that are commonly associated with extant forms of *conifers*. *Rostrumaspermum* can be best cited for such a reference where the seed bears archegonia having tubular neck identical with *Pinus laricio* and *P. sylvestris* where the archegonia bears a short tubular neck, too. Depiction of such *pineaceous* features in Triassic seed is indicative of that *coniferous* traits must have been differentiated during Triassic time through a transitional stage and also supports that the separation of modern *conifers* took place at this stage. Such macroplants are useful and serve as a link for intercontinental correlations.

Conclusions

In conclusion diverse affinities of superficially similar forms tremendously increase their usefulness in interpreting systematics and the time of origin of major groups of Gondwana flora. Characterization based upon assemblages of fertile organs increase our understanding of what general types of plants may have existed and broad data base for the initial formulation of ideas regarding paleofloristics all over the Gondwanic countries.

Remark. – Contributed to 3rd International Senckenberg Conference, Frankfurt am Main – 1990 on the occasion of Birth Centennary Celebrations of Richard KRÄUSEL: "International Symposium of Palaeobotany: Anatomical Investigations of Plant fossils".

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